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First blind daddy long-legs spiders from Australia and Réunion (Araneae, Pholcidae)

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Abstract

Daddy long-legs spiders are common inhabitants of tropical and subtropical caves around the globe. Numerous species have evolved troglomorphisms, including the loss of body pigments and eyes. Here we describe the first troglomorphic pholcids from Australia and Réunion. *Belisana coblynau* Huber & Clark, **sp. nov.** was extracted from mining boreholes in the arid West Australian Pilbara region. It represents a genus that is widespread in tropical forests of South and Southeast Asia, reaching the tropical north and east of Australia. *Belisana coblynau* is thus presumably a relict whose epigean ancestor lived in the area before the aridification of Australia starting in the early Cenozoic. *Buitinga ifrit* Huber & Cazanove, **sp. nov.** was collected in Grotte de La Tortue on Réunion, one of the oldest lava tubes on the island (~300,000 years). Congeneric species are known from East Africa, and the genus does not seem to have reached Madagascar. Since Pholcidae do not balloon, the now extinct epigean ancestor of *Buitinga ifrit* probably reached the island by highly accidental means (such as rafts or storms).

Keywords

Lava tube, mining borehole, relict, scrape sample, subterranean, troglomorphism

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Introduction

Spiders are in many ways preadapted to a hypogean life: most species rely on mechanical and chemical rather than on visual stimuli, and many species are therefore nocturnal; most spiders endure long periods of starvation, reflecting a low demand of energy; and many species are adapted to near ground microhabitats such as the leaf litter, which share certain characteristics with caves (Foelix 2011; Mammola and Isaia 2017). Among spiders, Pholcidae are one of the most likely groups to be encountered in caves around the globe, in particular in tropical and subtropical regions. A recent review of cave-dwelling pholcid spiders (Huber 2018) found that pholcids have been collected in about 1000 caves, and approximately one fourth of the currently ~1900 described species have been found in caves. However, most of these records are from species that do not appear to be troglomorphic in any obvious way; only 86 species were listed as troglomorphic. Of these, 42 were characterized as "strongly troglomorphic", i.e. without or with reduced eyes (Huber 2018).

An intriguing pattern in subterranean animals is that the large majority of them belong to a relatively small number of major taxa (e.g., Christiansen 2012; Moldovan 2012). This is also the case within Pholcidae: the large majority of troglomorphic Pholcidae are representatives of only two subfamilies: Pholcinae and Modisiminae; the other three subfamilies contain 17% of the known species but only 5% of the troglomorphic species (Huber 2018). This has been thought to explain the apparent absence of troglomorphic Pholcidae in Australia: the large majority of Pholcidae species in Australia are representatives of Arteminae (genera *Pholcitrichocyclus* Ceccolini & Cianferoni, 2022 and *Wugigarra* Huber, 2001), and for unknown reasons, Arteminae around the globe appear extremely unlikely to evolve troglomorphic species. For example, *Physocyclus* Simon, 1893 is a species-rich genus in Mexico, a country with countless caves and numerous troglomorphic Modisiminae (Huber 2018); however, not a single troglomorphic species of *Physocyclus* is known to exist. In Australia, a few representatives of Pholcinae have been described but these were previously thought to be restricted to tropical regions in northern and eastern Australia; they were thought to be relatively recent introductions from SE Asia and New Guinea (Huber 2001). The present finding of a blind *Belisana* Thorell, 1898 (Pholcinae) in the Pilbara supports the idea that Pholcinae rather than Arteminae will be found in available subterranean Australian habitats. At the same time, it refutes the idea that Pholcinae in Australia are restricted to the tropical north and east of the continent.

Another striking observation in troglomorphic pholcid spiders is their over-representation on islands (Huber 2018). Apart from Mexico, which is home to 45% of all known troglomorphic pholcids, most remaining species occur on islands: Jamaica, Canary Islands, Galápagos, Cuba, Madagascar, and Réunion. Since 2018, only one further eyeless pholcid has been described, again from an island (Galápagos; Huber et al. 2022). The eyeless pholcid from Réunion described below was already mentioned in the review of Huber (2018) but it is here formally described.

Materials and methods

Collecting methods

Specimens of *Belisana coblynau* Huber & Clark, sp. nov. were collected by scrape sampling. This method is commonly used to collect troglofauna, particularly when sampling for environmental impact assessments associated with mining (Halse and Pearson 2014). Due to regulations by the Environment Protection Authority (EPA) in Western Australia, new bores that are drilled for mining exploration purposes can only be sampled after six months; as a result, the boreholes were at least six months old at the time of sampling. A weighted net was lowered down uncased holes (diameter 150 mm). The net was lowered to the base of the hole or to the groundwater table (~35 m below ground level) and then drawn slowly back to the surface, "scraping" the net up the wall of the bore, knocking any fauna into the net. This was repeated four times, once on each of the four sides of the bore (i.e., north, south, east, and west). The samples were washed into a 250 ml plastic vial and preserved in 100% ethanol. Samples were stored at 4 °C. *Buitinga ifrit* Huber & Cazanove, sp. nov. was collected manually; specimens were preserved in 70% ethanol and stored at room temperature.

Repositories

The specimens are deposited in the following institutions: Museum d'Histoire Naturelle de La Réunion, Saint Denis (**MHNR**); Western Australian Museum, Perth (**WAM**); and Zoological Research Museum Alexander Koenig, Bonn (**ZFMK**).

Morphology and taxonomy

Taxonomic descriptions follow the style of publications on related Pholcidae taxa (i.e., Huber 2003, 2005; based on Huber 2000). Measurements were done on a dissecting microscope with an ocular grid and are in mm unless noted otherwise. Photos were made with a Nikon Coolpix 995 digital camera (2048 × 1536 pixels) mounted on a Nikon SMZ 18 stereo microscope or a Leitz Dialux 20 compound microscope. CombineZP (https://combinezp.software.informer.com/) was used for stacking photos. Drawings are partly based on photos that were traced on a light table and later improved under a dissecting microscope, or they were directly drawn with a Leitz Dialux 20 compound microscope using a drawing tube. Cleared epigyna were stained with chlorazol black. Abbreviations used in figures only are explained in the figure legends. Abbreviations used in the text: ALS = anterior lateral spinneret(s); a.s.l. = above sea level; L/d = length/diameter.

CO1 barcodes

DNA sequencing of the CO1 gene was conducted on all three *Belisana* specimens collected from the Pilbara, Western Australia. Our effort to extract DNA from *Buitinga*

specimens failed. Legs were dissected off the animals for DNA extractions using a Qiagen DNeasy Blood & Tissue kit (https://www.qiagen.com/ie). Elute volumes varied from 40 µl to 200 µl depending on condition and quantity of material. Primer combinations used for PCR amplifications were LCO1490:HCOoutout (Folmer et al. 1994; Schwendinger and Giribet 2005). Dual-direction, Sanger sequencing was undertaken for PCR products by the Australian Genome Research Facility (AGRF). The sequences were edited and aligned in Geneious (Kearse et al. 2012). The three newly sequenced barcodes of *Belisana coblynau* together with the CO1 barcodes of 19 *Belisana* species taken from Eberle et al. (2018) were translated into protein sequences using BioPython (version 1.78) (Cock et al. 2009) with invertebrate mitochondrial genetic code. Next, protein-MSAs were constructed using the mafft-linsi algorithm of MAFFT (version 7.487) (Katoh and Standley 2013), which then assisted the construction of nucleotide level MSAs with pal2nal.pl (Suyama et al. 2006). This helps avoid the introduction of biologically meaningless frameshifts to the alignments (Suyama et al. 2006). The genetic distances between different specimens were calculated based on the Kimura 2-parameter (K2P) model (Kimura 1980) using MEGA11 (Tamura et al. 2021), in which ambiguous positions for each sequence pair were deleted. An initial effort to combine the *Belisana coblynau* sequences with all CO1 Pholcinae sequences from Eberle et al. (2018) and to calculate maximum-likelihood trees was abandoned. The preliminary results from untrimmed and trimmed datasets were highly inconsistent and the suggested affinities not credible (e.g., *Belisana coblynau* nested in the New World endemic genus *Metagonia* Simon, 1893).

Results

Taxonomy

***Belisana coblynau* Huber & Clark, sp. nov.**
https://zoobank.org/50A34349-C82F-49FA-8679-77C8CCC86D1B
Figs 1, 2

Type material. Australia – Western Australia • ♂ holotype; ~85 km ESE Pannawonica; 21.8836°S, 117.1211°E; 590 m a.s.l.; 25 Jun. 2019; M.D. Scanlon and H.L. Clark leg.; WAM T158896.

Type locality. Australia, Western Australia, ~85 km ESE Pannawonica, 21.8836°S, 117.1211°E, 590 m a.s.l.

Type specimen. Holotype male, in ethanol. Original labels: "WA: JSE, ca 87 km ESE Pannawonica, 21°53'43.450"S, 117°07'48.63"E (GDA 94) 25. Jun. 2019, Scanlon MD, Clark HL (KRC 0364), Trog scrape, 35 m", "KRC0364", "WAM T 158896", "100% EtOH".

Other material examined. Australia – Western Australia • 1 ♀, assigned tentatively, see Remark below; same locality as holotype but 3.7 km NW; 21.8583°S, 117.0972°E; 540 m a.s.l.; 25 Apr. 2019; M.D. Scanlon and H.L. Clark leg.;

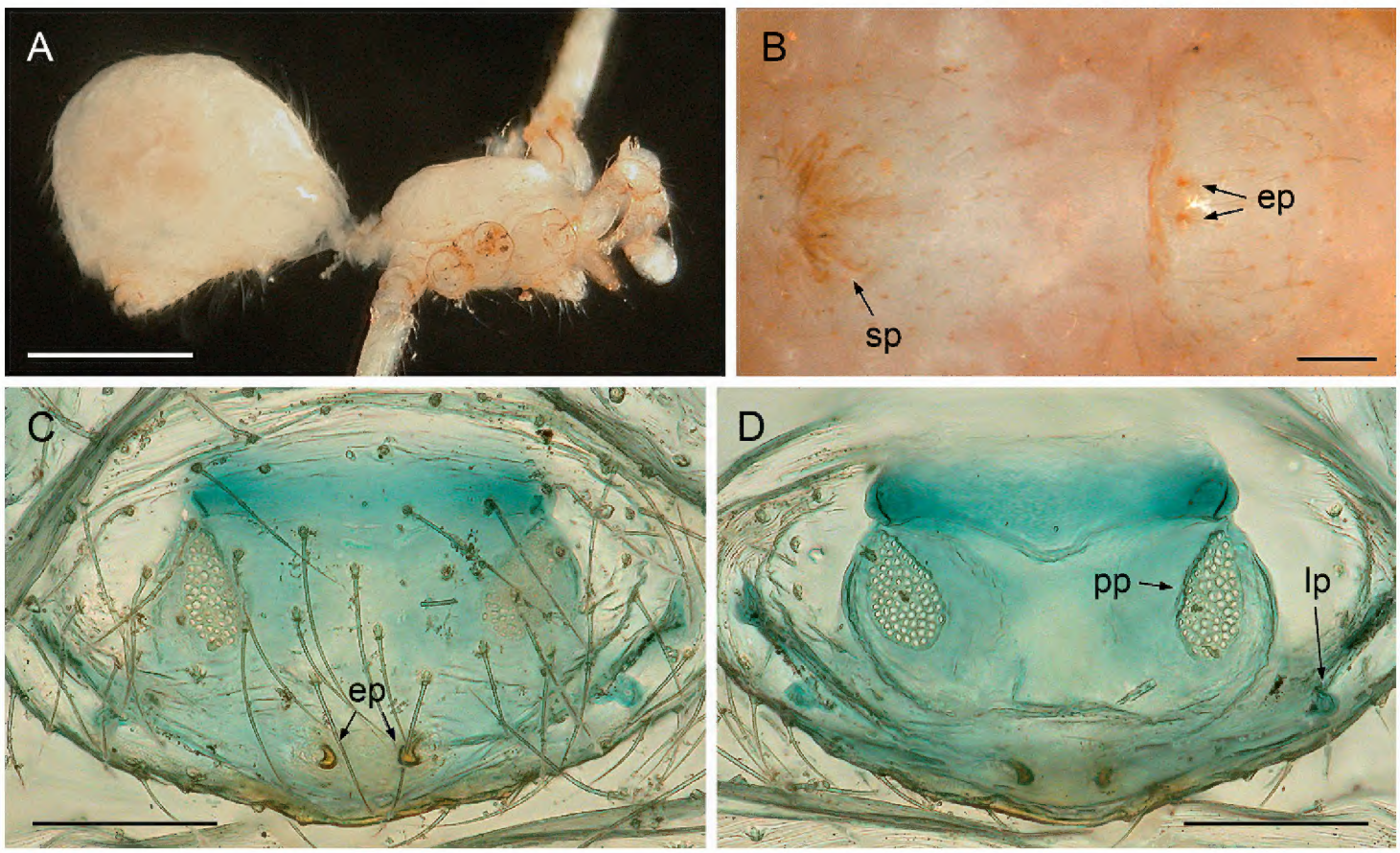

Figure 1. *Belisana coblynau* Huber & Clark, sp. nov., male holotype and female, WAM T158896–7 **A** male habitus, lateral view **B** female abdomen, ventral view **C, D** cleared female genitalia, ventral and dorsal views. Abbreviations: ep, epigynal pockets; lp, lateral pocket; pp, pore plate; sp, spinnerets. Scale bars: 0.5 mm (**A**); 0.1 mm (**B–D**).

"KRC0226", WAM T158897 • 1 juv.; same locality as holotype but 1.6 km SE; 21.8954°S, 117.1302°E; 570 m a.s.l.; 26 Apr. 2019; M.D. Scanlon and H.L. Clark leg.; "KRC0254", WAM T158895.

Remark. The genetic distance (Table 1) between the male holotype and the juvenile specimen was 0.5%, strongly suggesting that the two are conspecific. The distances between these two specimens and the female was much higher, at 8.5 and 8.8%, respectively. This is within a range that in Pholcidae is always problematic due to the overlap of intra- and interspecific genetic (CO1) variation between approximately 8 and 11% (Astrin et al. 2006; Huber et al. in press). In the case of the female, we are thus unsure about its taxonomic status.

Diagnosis. Distinguished from known congeners (and other Pholcinae) by details of procursus (Fig. 2D, E; straight, with simple retrolateral process, bifid prolateral process, and widened membranous tip), genital bulb (Fig. 2A, B; bulbal apophysis short and hooked, embolus straight and pointed at tip), male chelicerae (Fig. 2C; pair of light proximal processes; pair of simple distal frontal apophyses without modified hairs), epigynum (Fig. 1B; protruding, with pair of pockets close together), and female internal genitalia (Figs 1C, D, 2F; pore plates wide apart; distinctive pair of additional internal lateral pockets).

Description. Male (holotype). ***Measurements.*** Total body length ~1.5–1.6 (abdomen detached), carapace width 0.60. Leg 1: 11.5 (2.9 + 0.2 + 3.0 + 4.4 + 1.0); legs 2 and 3 missing; tibia 4: 2.3; tibia 1 L/d: 50.

Table 1. GenBank accession numbers and genetic distances. CO1 accession numbers of the three *Belisana coblynau* specimens and genetic distances (K2P) among them and other *Belisana* species taken from Eberle et al. (2018).

Taxon	OQ525972	OQ525971	OQ525973
OQ525972, *Belisana coblynau* male			
OQ525971, *Belisana coblynau* female	0.088		
OQ525973, *Belisana coblynau* juvenile	0.005	0.085	
S127_Belisana_Bor152_Bor166	0.277	0.261	0.277
S249_Belisana_Mal91_Mal290	0.285	0.283	0.287
S242_Belisana_leuser_Mal304	0.233	0.241	0.233
S247_Belisana_Mal76_Mal278	0.274	0.299	0.276
S498_Belisana_minneriya_SL123	0.238	0.245	0.236
S248_Belisana_Mal77_Mal279	0.277	0.274	0.275
S103_Belisana_Tai4_Tai67	0.233	0.264	0.231
S230_Belisana_australis_Phi280	0.244	0.264	0.244
S125_Belisana_Bor121_Bor198	0.227	0.241	0.225
S244_Belisana_Mal30_Mal241	0.255	0.269	0.259
S333_Belisana_bohorok_Ind127	0.250	0.250	0.248
S336_Belisana_nahtanoj_Ind181	0.209	0.212	0.208
S338_Belisana_tambligan_Ind213	0.237	0.234	0.234
S339_Buitinga_buhoma_Uga124	0.254	0.269	0.251
S340_Buitinga_ruhiza_Uga122	0.252	0.262	0.247
S341_Buitinga_ruwenzori_Uga156	0.255	0.269	0.249
S334_Belisana_Ind15_Ind140	0.274	0.256	0.274
S386_Belisana_sabah_Bor214	0.235	0.250	0.233
S417_Belisana_ranong_Mal361	0.210	0.215	0.210

Color (in ethanol). Entire specimen pale ochre to whitish (Fig. 1A).

Body. Habitus as in Fig. 1A. Ocular area not raised, without any remnants of eye pigment and lenses. Without thoracic groove. Clypeus unmodified. Sternum wider than long (0.40/0.30), unmodified. Abdomen globular, conical at spinnerets.

Chelicerae. As in Fig. 2C, with pair of light proximal processes, pair of simple distal frontal apophyses without modified hairs (distance between tips: 50 μm), without stridulatory files.

Palps. As in Fig. 2A, B; coxa unmodified, trochanter with low rounded retrolateral ventral protrusion, femur cylindrical, without process; tibia with only one (retrolateral distal) trichobothrium; procursus (Fig. 2D, E) straight, with simple retrolateral process, bifid prolateral process, and widened membranous tip; genital bulb with short hooked bulbal apophysis and straight embolus pointed at tip.

Legs. Apparently without spines and curved hairs (most hairs on available legs missing); leg trichobothria not seen; tarsus 1 with ~10 pseudosegments, barely visible in dissecting microscope.

Female. In general similar to male, but larger (in particular the abdomen); total body length 1.8; carapace width 0.62; most legs detached (tibia 4: 2.6). Epigynum (Fig. 1B) main anterior plate semicircular, with distinct pair of pockets (distance between pockets: 30 μm), in lateral view protruding. Internal genitalia (Figs 1C, D, 2F)

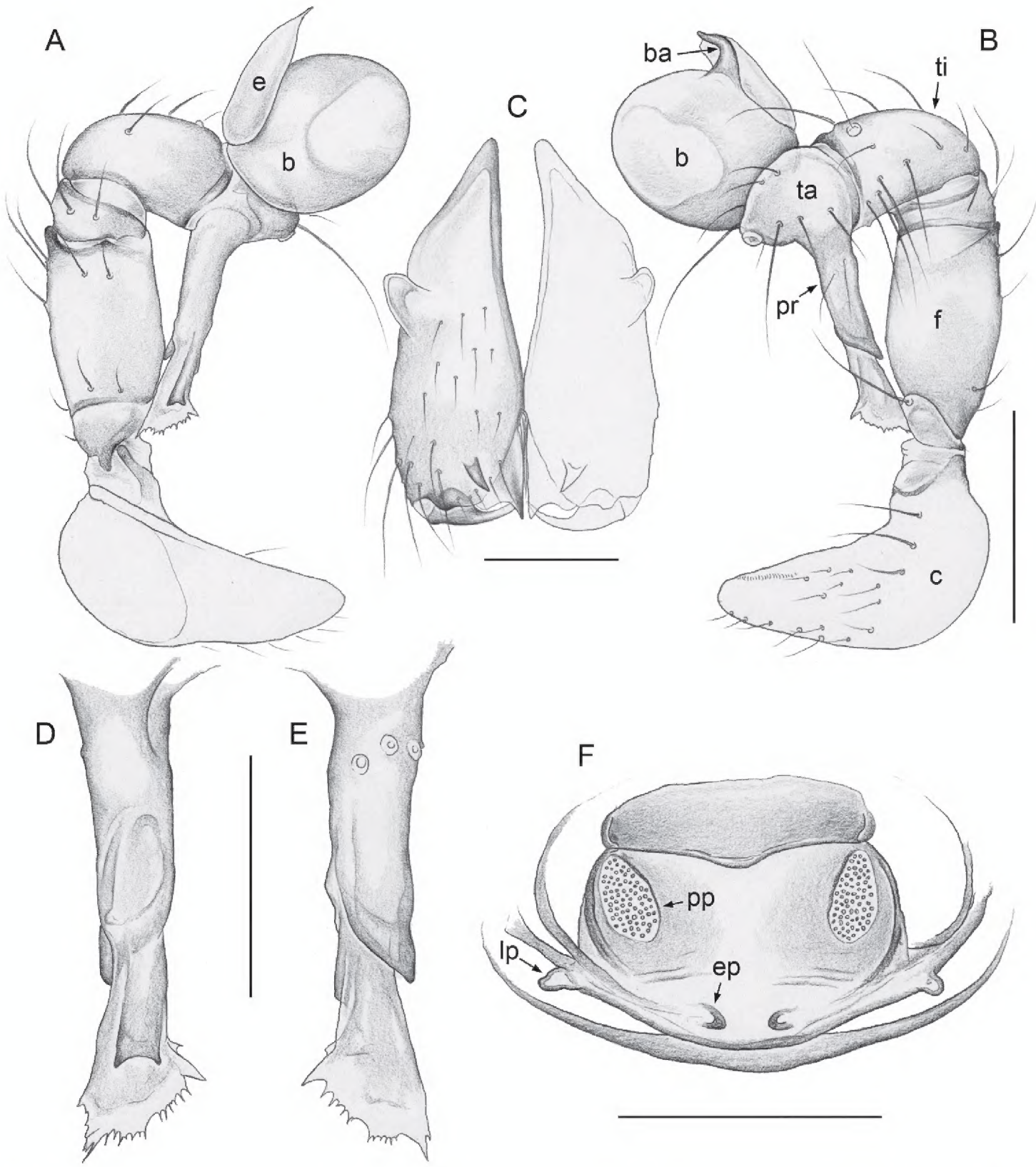

Figure 2. *Belisana coblynau* Huber & Clark, sp. nov., male holotype and female, WAM T158896–7 **A, B** left male palp, prolateral and retrolateral views **C** male chelicerae, frontal view **D, E** left procursus, prolateral and retrolateral views **F** cleared female genitalia, dorsal view. Abbreviations: b, genital bulb; ba, bulbal apophysis; c, coxa; e, embolus; ep, epigynal pocket; f, femur; lp, lateral pocket; pp, pore plate; pr, procursus; ta, tarsus; ti, tibia. Scale bars: 0.2 mm (**A, B, F**); 0.1 mm (**C–E**).

with pair of pore plates wide apart, distinctive pair of additional internal lateral pockets. Each ALS with 3–4 small cylindrical spigots in addition to large widened spigot and long pointed spigot (checked in cleared abdomen).

Etymology. The species epithet refers to the mythical gnome-like creatures that are said to haunt mines and quarries (of Wales and beyond); noun in apposition.

Distribution. Known from three neighboring (within 5 km) localities in Western Australia.

Natural history. The spiders were extracted from mining bores in the Hamersley Range using scrape sampling (Fig. 5A–C). This collecting method precludes gaining detailed natural history data. The specimens were collected between ground level and approximately 35 m below ground level. The temperature in these holes at 15 m below ground level was constant at 32–33 °C. For a general characterization of the Pilbara troglofauna, see Discussion.

Buitinga ifrit Huber & Cazanove, sp. nov.

https://zoobank.org/094155C6-26E5-47A3-8D88-AE84E1D7873D

Figs 3, 4

Buitinga? sp. nov. "Reun1": Huber 2018: 4.

Type material. Réunion – Saint-Paul • ♂ holotype; Grotte (Caverne) de la Tortue; 21.0743°S, 55.2491°E; ~220 m a.s.l.; 9 Mar. 1997; J.-C. Ledoux leg.; ZFMK (Ar 24187).

Type locality. Réunion, Saint-Paul, Grotte (Caverne) de la Tortue, 21.0743°S, 55.2491°E, ca 220 m a.s.l.

Type specimen. Holotype male, in ethanol. Original label: "St. Paul, grotte de la Tortue, Pholcidae (sur toile) 9/3/1997".

Other material examined. Réunion – Saint-Paul • 1 ♂ 6 ♀ (+ 1 juv.) paratypes; same data as for holotype; MHNR • 1 ♀ paratype (+ 1 juv.); same locality as for holotype, Salle du Muséum; 13 Jul. 1996; C. Guillermet leg.; between stones from scree which obstruct the bottom of the gallery, "2022.E.6.2"; ZFMK (Ar 24188) • 1 ♀ paratype; same locality as for holotype; Salle du Muséum; 24 Feb. 2007; S. Gasnier leg.; on the ground, "CT/070124.004" "2011.E.65.1"; MHNR.

Diagnosis. Distinguished from known congeners (and other Pholcinae) by strong bifid process on male palpal trochanter (Fig. 4B), by details of procursus (Fig. 4E, F; short main branch curved towards dorsal and with deeply bifid tip, large and mostly membranous side branch originating from ventral side of main branch, with complex tip), genital bulb (Fig. 4A; bulbal apophysis slender and weakly curved, with small process at basis, embolus cylindrical), male chelicerae (Fig. 4C, D; pair of light proximal processes; pair of distal frontal apophyses with four modified hairs each), epigynum (Fig. 3B; barely protruding, without pockets, distinctive median posterior process only visible in cleared specimens), and female internal genitalia (Figs 3C, D, 4G; oval pore plates; pair of dark lateral structures).

Description. Male (holotype). ***Measurements.*** Total body length 2.0, carapace width 0.70. Leg 1: 18.5 (4.6 + 0.3 + 5.1 + 7.3 + 1.2); tibia 2: 3.1; tibia 3: 1.9; tibia 4: 2.8; tibia 1 L/d: 85.

Color (in ethanol). Entire specimen pale ochre to whitish (Fig. 3A).

Body. Habitus as in Fig. 3A. Ocular area slightly raised, without any remnants of eye pigment and lenses. Without thoracic groove. Clypeus unmodified. Sternum wider than long (0.50/0.40), unmodified. Abdomen oval, conical at spinnerets.

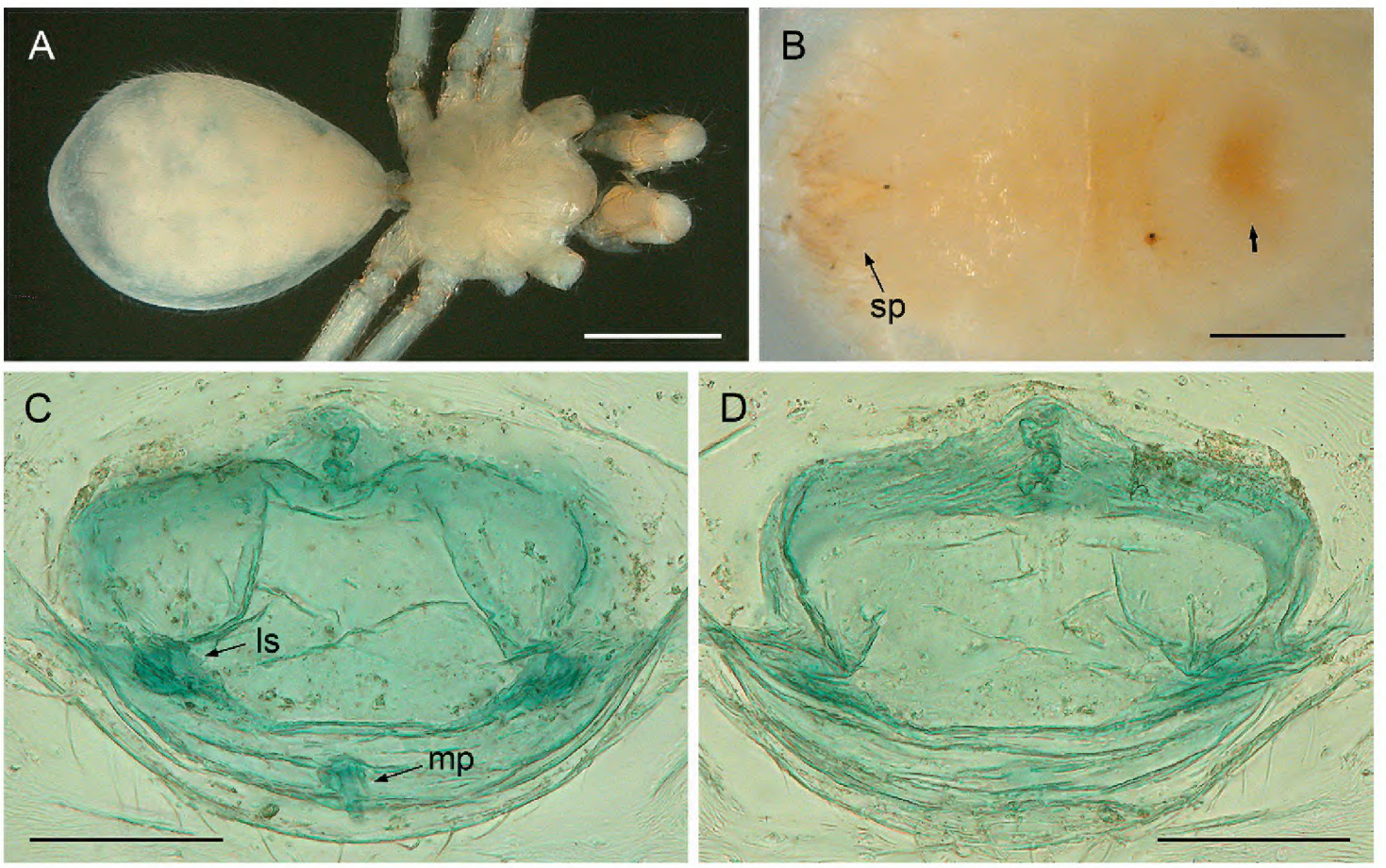

Figure 3. *Buitinga ifrit* Huber & Cazanove, sp. nov., male holotype and female paratype, ZFMK (Ar 24187–88) **A** male habitus, dorsal view **B** female abdomen, ventral view (arrow: darker median area) **C, D** cleared female genitalia, ventral and dorsal views. Abbreviations: ls, dark lateral structure; mp, median posterior process; sp, spinnerets. Scale bars: 0.5 mm (**A**); 0.2 mm (**B**); 0.1 mm (**C, D**).

Chelicerae. As in Fig. 4C, with pair of light proximal processes and pair of distal frontal apophyses with four modified hairs each (Fig. 4D); without stridulatory files.

Palps. As in Fig. 4A, B; coxa unmodified, trochanter with strong bifid process, femur short, slightly widening distally, without process; tibia with two trichobothria; procursus (Fig. 4E, F) complex, with short main branch curved towards dorsal and with deeply bifid tip, large and mostly membranous side branch originating from ventral side of main branch, with complex tip; genital bulb with slender and weakly curved bulbal apophysis with small process at basis, and cylindrical embolus with transparent fringes at tip.

Legs. Apparently without spines and curved hairs (many hairs missing); few short vertical hairs; leg trichobothria and pseudosegments not seen.

Variation (male). Second male apparently indistinguishable; legs 1 missing.

Female. In general similar to male; total body length 1.8–2.0; carapace width 0.68–0.72; tibia 1 in seven females: 3.7–4.7 (mean 4.1). Epigynum (Fig. 3B) main anterior plate slightly protruding, barely visible in ventral view, with darker median area, without pockets, with distinctive median posterior process (Fig. 4H, I) only visible in cleared specimens. Internal genitalia (Figs 3C, D, 4G) with barely visible oval pore plates and pair of dark lateral structures. Each ALS apparently with only two spigots (large widened spigot and long pointed spigot; checked in cleared abdomen).

Etymology. The species epithet refers to a demon in Islamic mythology that is often associated with the underworld; noun in apposition.

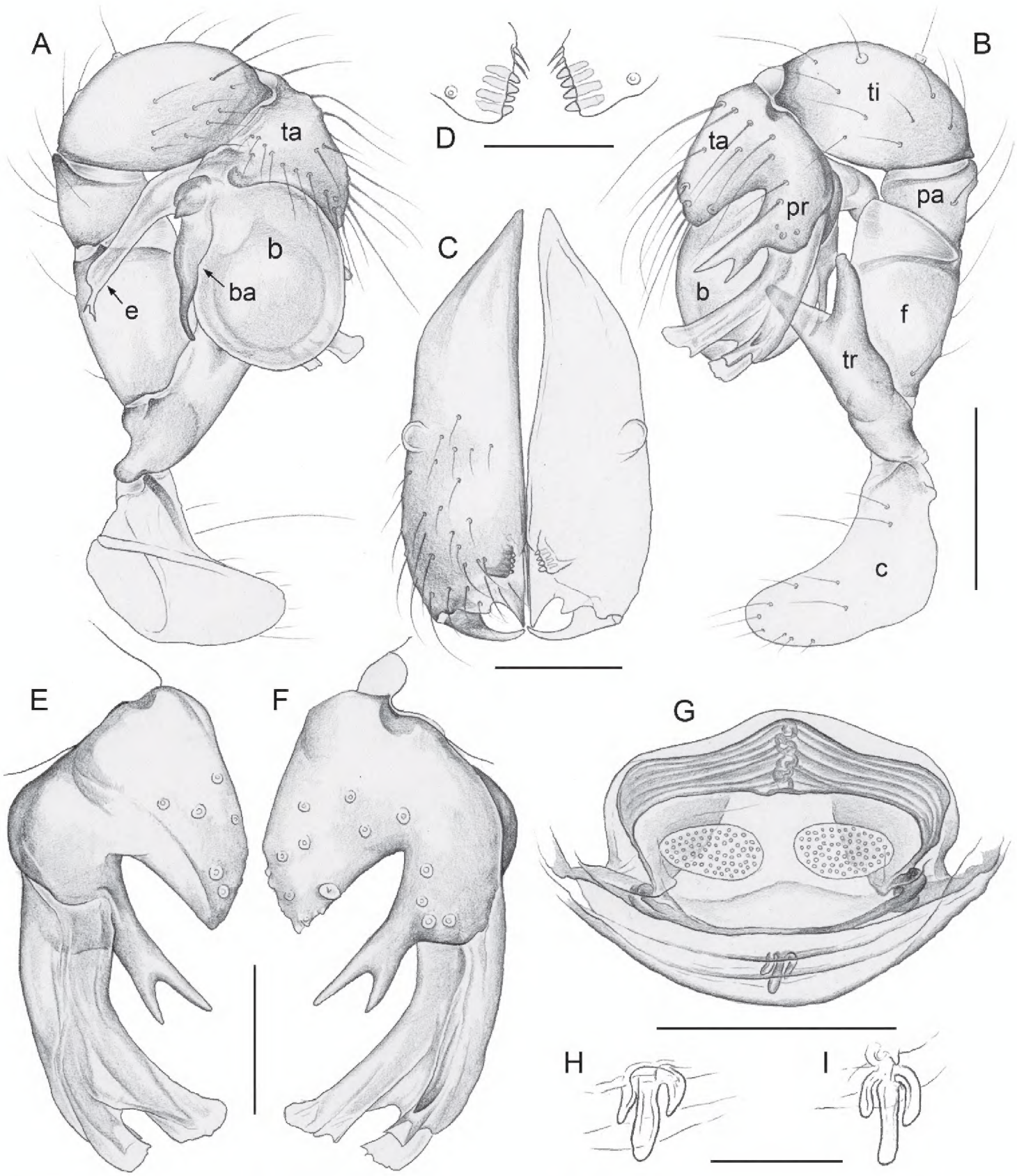

Figure 4. *Buitinga ifrit* Huber & Cazanove, sp. nov., male holotype and female paratype, ZFMK (Ar 24187–88) **A, B** left male palp, prolateral and retrolateral views **C, D** male chelicerae, frontal view, and frontal male cheliceral apophyses in more detail **E, F** left tarsus and procursus, prolateral and retrolateral views **G–I** cleared female genitalia, dorsal view, and posterior median structure in two cleared specimens in more detail. Abbreviations: b, genital bulb; ba, bulbal apophysis; c, coxa; e, embolus; f, femur; pa, patella; pr, procursus; ta, tarsus; ti, tibia; tr, trochanter. Scale bars: 0.2 mm (**A, B, G**); 0.1 mm (**C, E, F**); 0.05 mm (**D, H, I**).

Distribution. Known from type locality only.

Natural history. The spiders were collected deep within the Grotte de la Tortue lava tube (Fig. 5D, E). Some of the specimens were collected in the Salle du Muséum,

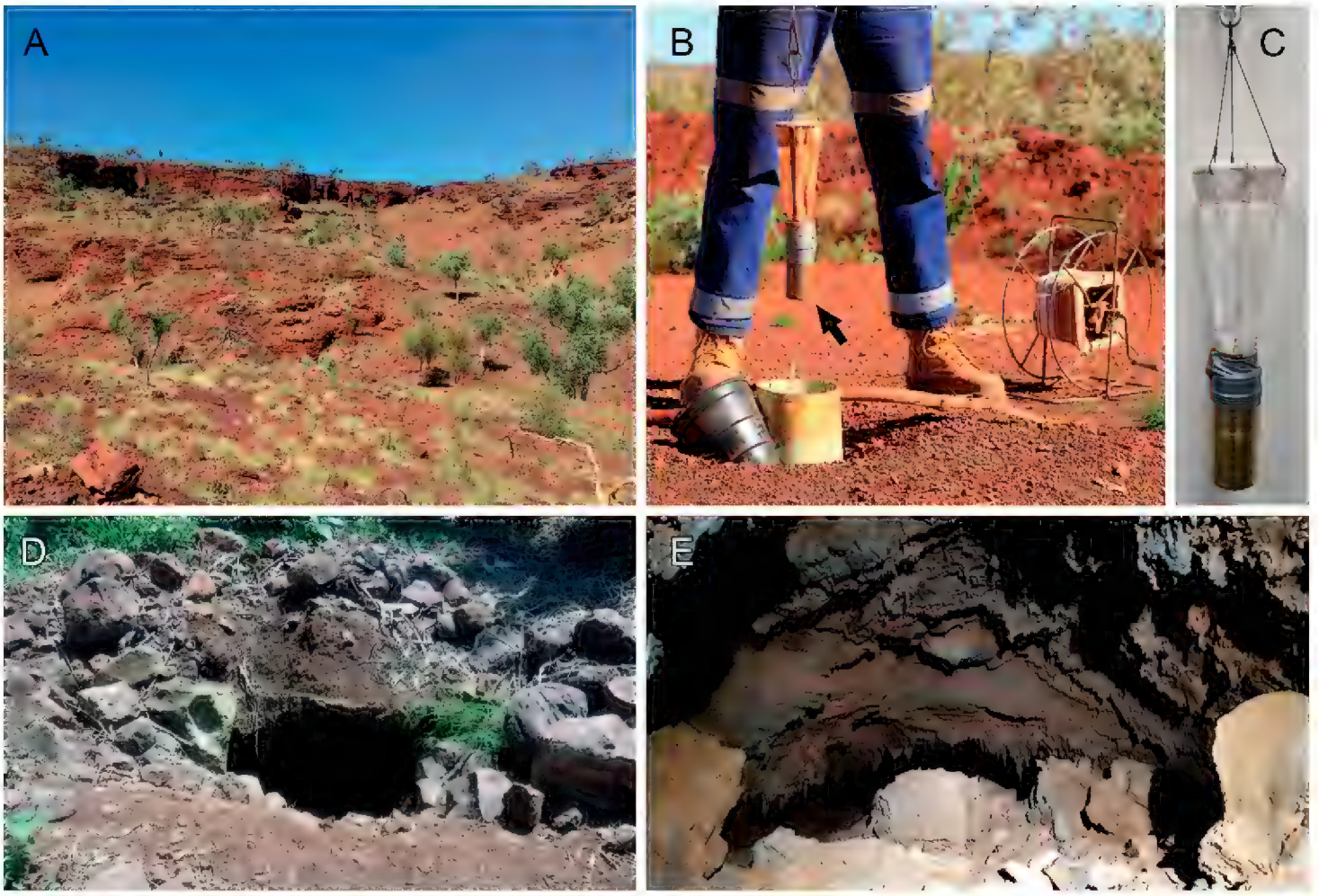

Figure 5. Epigean and hypogean habitats and collecting method **A** Hamersley Range in Western Australia; the area of the sampled boreholes **B** weighted net (arrow) above a borehole **C** weighted net used for scrape sampling **D** main entrance of the Grotte de La Tortue (photo T. Percheron, 2015) **E** gallery of the lost goat in Caverne de La Tortue (photo T. Percheron, 2022).

a section that is about 150 m from the cave entrance (see topographic map in Hoch et al. 2003). They were found among rocks on the ground. For the other specimens, cave section and microhabitat are unknown. For a general characterization of the caves and cave fauna of Réunion, see Discussion.

Discussion

Generic placements and their implications

The taxonomic assignments of the new species to the genera *Belisana* Thorell, 1898 and *Buitinga* Huber, 2003 are not immediately obvious and need some justification, especially since this affects the biogeographic interpretation. Both species are clearly representatives of Pholcinae, based on the proximal lateral processes on the male chelicerae. Within Pholcinae, they are very likely representatives of what has been called Pholcinae 'group 1' or 'group 2' (Huber et al. 2018), i.e. Pholcinae without a distinct sclerite connecting the male genital bulb to the tarsus. These two groups together currently count 16 genera.

For the new Australian species, numerous genera of Pholcinae 'group 1' and 'group 2' can be ruled out easily: several have only two spigots on each ALS (*Aetana* Huber, 2005; *Hantu* Huber, 2016; *Khorata* Huber, 2005; *Paramicromerys* Millot, 1946; *Savarna* Huber, 2005; *Spermophorides* Wunderlich, 1992; *Wanniyala* Huber & Benjamin, 2005); in some genera, the genital bulb has only one process, the embolus (*Anansus* Huber, 2007; *Giloloa* Huber, 2019; *Metagonia* Simon, 1893; *Nyikoa* Huber, 2007; *Tangguoa* Yao & Li, 2021); females of *Spermophora* Hentz, 1841 have one or two copulatory pockets behind the epigynum; in *Buitinga*, males have frontal cheliceral apophyses with modified hairs and females have an epigynal scape; and in *Zatavua* Huber, 2003 males, the lateral cheliceral apophyses point backwards and there is a retrolateral notch on the palpal tarsus. This leaves only *Belisana*, which is, together with *Spermophora*, the only member of Pholcinae 'group 1' and 'group 2' known to occur in Australia. However, no known species of *Belisana* has a procursus that has a specific similarity with the procursus of *Belisana coblynau* Huber & Clark. The large genetic distances to all other sequenced *Belisana* species (and to other Pholcinae) support the isolated position of this species. Clearly, more molecular data are needed to support or refute our generic assignment. However, the main conclusion is unaffected by the exact generic placement: *Belisana coblynau* is a relict species. Except for *Belisana coblynau*, all extant Australian Pholcinae are restricted to the tropical north and east of the continent (Huber 2001, maps 15–19). Certain Pholcinae taxa must have been present in Australia before the climate became drier and more seasonal between 25 and 10 Ma (Martin 1994), or at least before severe aridity set in during the Pliocene (5–2 Ma) (Bowler 1982; Crisp et al. 2004).

Belisana coblynau is the fourth troglomorphic representative of the genus; the three other species are from Thailand, Laos, and Vietnam (Huber 2018). Compared to a sample of 146 described and undescribed congeners (B.A. Huber, unpublished data), *B. coblynau* is close to the mean values regarding carapace width, tibia 1 length, and metatarsus 1 length. With respect to body size and leg length, the species is thus apparently not troglomorphic.

For the new species from Réunion, most of the possible genera can also be ruled out easily. The following is a selection of diagnostic characters: in numerous genera, frontal male cheliceral apophyses are either absent or they have no modified hairs (*Aetana*, *Anansus*, *Belisana*, *Giloloa*, *Hantu*, *Khorata*, *Nyikoa*, *Savarna*, *Tangguoa*); in some genera, females consistently have epigynal or abdominal copulatory pockets (*Anansus*, *Belisana*, *Nyikoa*, *Paramicromerys*, *Spermophorides*, *Spermophora*, *Zatavua*); in some genera, the ALS have numerous (5–6) spigots rather than only two (*Anansus*, *Nyikoa*, *Zatavua*); in some genera, the genital bulb has only one process, the embolus (*Anansus*, *Giloloa*, *Metagonia*, *Nyikoa*, *Tangguoa*); all known representatives of *Wanniyala* have a modified male clypeus and long and widely spaced frontal cheliceral apophyses. This leaves only *Buitinga* (incl. its sister group, a clade of misplaced East African "*Spermophora*"; Huber et al. 2018), an East African genus in which males of most species have cheliceral apophyses that are very similar to those of the newly described species and in which females are characterized by a scape (even though the shape of the scape in *Buitinga ifrit* Huber & Cazanove is unique). Surprisingly, however, no known *Buitinga* in East Africa has a procursus that has a specific similarity with the unique procur-

sus of *Buitinga ifrit*. If our generic assignment is correct, then the ancestor of *Buitinga ifrit* must have reached Réunion from East Africa within the last few million years. This is remarkable for two reasons: first, Pholcidae do not easily reach Far Islands (Huber and Meng 2023); second, *Buitinga* is not known to occur on Madagascar. *Buitinga ifrit* is the only known troglomorphic representative in the genus.

Australian troglofauna without caves

According to White (1988), a cave can be defined as "a natural opening in the Earth, large enough to admit a human being, and which some human beings choose to call a cave". The Pilbara (and Yilgarn) troglofauna is unique in that it inhabits a landscape devoid of caves that would fit White's definition (Halse 2018a, b). Instead, these animals occupy faults, fractures, and voids that form micro-caverns (<5 mm width) and meso-caverns (5–500 mm), which are widespread throughout the landscape (Howarth 1983). These subterranean spaces occur in the host rock of the vadose zone, defined as the space between ~2 m below the ground surface and the water table (Halse and Pearson 2014). The main mechanism resulting in these subterranean spaces is weathering. It is caused largely by water flow, temperature change and animal movement. The related mineralization process whereby minerals are leached from some areas of host rock to enrich other areas can also create voids (Morris 1983). Due to the extreme age of the Pilbara (ca. 3,660–2,800 Ma; Wellman 2000), there are extensive areas within rock formations where subterranean spaces appropriate for subterranean fauna have developed (Johnson 2009).

The Hamersley Range is one of the most prominent features in the Pilbara landscape, and consists largely of exposed banded iron formation (Fig. 5A), a geology known to have been extensively weathered and to contain suitable habitat for troglofauna (Johnson and Wright 2001). These environments have a stable temperature and constant humidity (Moldovan et al. 2018), in contrast to surface conditions where high temperatures and dry conditions are commonplace. It has been suggested that the troglofauna of this region has been forced into the subterranean world by the aridification of the Australian continent (Humphreys 2000; Harvey et al. 2008). Early in the Cenozoic, water was plentiful throughout Australia, but over the course of ~60 Ma, the majority of inland surface water has been lost, with accelerating aridification in the last 33 Ma (Mabbutt 1977; Crisp et al. 2004; Owen et al. 2017). The absence of light and the minimal availability of organic matter (Moldovan et al. 2018) has led to the usual adaptations seen in cave animals: deficient pigmentation, reduced or absent eyes, vermiform bodies, elongate sensory structures, loss of wings, increased lifespan, K-selected breeding strategies, and decreased metabolic rates (Gibert and Deharveng 2002).

Troglofaunal spiders of the Pilbara are estimated to have ranges of between 1 and ~1,400 km^2 (Halse and Pearson 2014) with a median linear range of 2.2 km (Halse 2018b). For comparison, troglofaunal isopods are understood to have a median range of 1.8 km while dipterans and hemipterans have greater median ranges of 68 and 159 km, respectively (Halse 2018b). The vast majority of troglofauna species have small ranges (< 10,000 km^2) and meet Harvey's (2002) criteria of Short-Range Endemism (SRE).

The Pilbara is one of the richest regions of the world for troglofauna, with over 1,500 species estimated as of 2018 (Halse 2018b). Approximately 7% of collected species from the Pilbara are spiders (Halse 2018b). At least 91 species of spiders are represented within the troglofauna of the Pilbara including the newly discovered pholcid (Bennelongia Environmental Consultants, unpublished data). Of these, the goblin spiders of the family Oonopidae are the most represented in both number of genera (6), number of species (50) and number of specimens (139). All of the described species of troglofaunal spiders of the Pilbara are goblin spiders, with eight species of *Prethopalpus* described by Baehr et al. (2012). Additionally, the goblin spider *Opopaea ectognophus* was described by Harvey and Edward (2007) along with two other species from the Cape Range and Kimberley regions of Australia, respectively. An additional goblin spider, *Pelicinus saaristoi* has been described by Ott and Harvey (2008) from Barrow Island, a subterranean fauna hotspot located off the Pilbara coast (Clark et al. 2021; Eberhard and Howarth 2021). Apart from these few studies, troglofaunal spiders of the Pilbara remain understudied and underrepresented in the scientific literature. Unpublished data suggest the presence of a rich spider fauna, including Gnaphosidae, Linyphiidae, Micropholcommatidae, Symphytognathidae, Tetrablemmidae, Theridiidae, and Trochanteriidae (Bennelongia Environmental Consultants, unpublished data).

Caves and cave fauna in Réunion

Réunion is a volcanic island and its underground environment is largely limited to lava tubes dating back to approximately 300,000 years (Sendra et al. 2017). Several large lava tubes at low altitudes are documented in Audra (1997). The Grotte de La Tortue volcanic tube is located on the northwestern side of the island, at the western base of the now inactive Piton des Neiges volcano. The cave is a lava tunnel system developed within vesicular basaltic lava. The ground hosting this cavity comes from the flows of phase II of the Piton des Neiges (estimated age between 2,100,000 and 430,000 years ago; Brial 1996). It is one of the oldest known caves on Réunion Island. With a maximum length of 322 meters, the cavern system is complex, with many branches and narrow sections (see topographic map in Hoch et al. 2003). The cumulative length of the galleries explored to date is approximately 690 m (Brial 1996). The main entrance is steep and accessible only by ladder or abseil; a second entrance is accessible only by crawling in the Gallery of the Toad. The first cavern forms a large chamber but quickly grades into narrow, shallow passages. At the main entrance, fallen blocks of basalt cover the ground but starting at approximately 2 m from the entrance, these are covered by very fine sediment (50–150 cm thick). This sediment is continuous through the cave system. The cave atmosphere is extremely humid (>97% according to Hoch et al. 2003). The temperature is 25–26 °C (Guillermet 1996; Cazanove and Mahé 2007). Some of the cave floor deposits show evidence of high-energy fluvial activity (ripple marks on shallow compact sediments). Brial (1996) speculated that a lake may form during heavy rains. According to Hume (2005), the cave was a natural pitfall trap for a number of endemic species because several animal bones were found, such as the fa-

mous Bourbon Giant Turtle, *Cylindraspis indica* (Schneider, 1783) and flightless birds (Mourer-Chauviré et al. 1999).

Despite a few studies (Rochat et al. 2003; Cazanove and Mahé 2007), the subterranean fauna on Réunion Island is still poorly known. Previously, only one troglobitic spider species has been known from the island: *Trogloctenus briali* Ledoux, 2004 (Ctenidae) (Rochat et al. 2003; Ledoux 2004), which is known from a single female specimen collected in Grotte de La Tortue. Other troglobites documented from Réunion include a planthopper (Hoch et al. 2003), Staphylinidae and Carabidae beetles (Jarrige 1957; Deuve 2007; Poussereau et al. 2011; Lecoq 2012) and a diplurid (Sendra et al. 2017). Unpublished records for the Grotte de La Tortue include unidentified representatives of Pseudoscorpiones, Acari, Myriapoda, Coleoptera, Blattoptera (Cazanove and Mahe 2007; G. Cazanove, unpubl. data), as well as two introduced spider species: *Eidmanella pallida* (Emerton, 1914) (Nesticidae) and *Loxosceles rufescens* (Dufour, 1820) (Sicariidae) (J.C. Ledoux, pers. comm. 2013).

Conclusions

The newly described *Belisana coblynau* Huber & Clark from the arid Pilbara in northwestern Australia is the first troglomorphic pholcid spider reported from the continent. It represents the subfamily Pholcinae, which was previously thought to be restricted to the tropical north and east of the continent. The new species suggests that Pholcinae were instead widely distributed in Australia before the continent's aridification in the last tens of millions of years.

The newly described *Buitinga ifrit* Huber & Cazanove from a lava tube on Réunion Island has its closest known relatives in eastern Africa. The genus *Buitinga* is not known to occur on Madagascar. Together with the age of Réunion (~3 Ma) and the Grotte de La Tortue lava tube (~300,000 years), this suggests that the epigean ancestor of *Buitinga ifrit* has reached Réunion relatively recently and by highly accidental means (such as rafts or storms), and that it adapted relatively quickly to the subterranean environment.

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